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Figure 1. Rainbow trout (***Oncorhynchus mykiss***), a fish that spits out mosses. Photo by Eric Engbretson, through Creative Commons.

Fish Uses of Bryophytes

At the onset, I wasn't sure I could make a chapter on the relationship between bryophytes and fish. I was sure I had read a long time ago that the aquatic moss ***Fontinalis*** (Figure 3) was found in the gut of a fish, but I couldn't locate the information again. So we tried our own experiments. We placed ***Fontinalis*** in a tank with rainbow trout (***Oncorhynchus mykiss***; Figure 1, Figure 2). The moss was colonized by aquatic insects, so we considered it a suitable source of food. But these starved rainbow trout ignored it. Finally, in desperation, the grad student doing this experiment tried to force feed the fish. Most of the time, even these "strike-at-anything" fish spit the moss back out. Finally the student managed to get the moss into the mouth and swallowed by force feeding. But the moss passed through the digestive tract undigested (Figure 47). It didn't look good for my hypothesis that fish might serve as upstream dispersal agents for stream bryophytes.

The rainbow trout is native to tributaries of the Pacific Ocean in North America and Asia. The juveniles hang out near the bottom whereas the adults occur more in open water. Although the fish may behave as an **anadromous** fish (living in the ocean and migrating up freshwater streams to spawn), this seems to be mostly an opportunistic behavior, with many populations never venturing to the ocean. They are known to seek areas of streams that have overhanging vegetation and to subsist on a diverse diet that includes aquatic insects (NRCS 2000). Given these criteria, it would seem that they could take advantage of the bryophytes, especially dangling ones such as ***Fontinalis*** species, for cover, especially for young fish. And aquatic mosses provide a rich habitat of aquatic insects and other invertebrates that could serve as food. So we must ask ourselves if there really is little connection between fish and bryophytes, or is it simply a neglected area of study. In this chapter we will examine the relationships that have been reported in the hope that they will stimulate further research into natural habitats and the role of the bryophytes in the lives of fish.

As you will soon read, my original contention that at least some fish, in some circumstances, eat bryophytes, is true. But bryophytes provide other roles, probably more important to the fish than their role as a food source. Based on the meager evidence I could locate, some fish use bryophytes for cover (especially small fish), spawning, and sources of invertebrates. Some even eat bryophytes.

Figure 2. Rainbow trout (***Oncorhynchus mykiss***), a commonly cultivated fish used for release to stock streams and lakes. These cultivated fish refused ***Fontinalis***, even when it had insects living on it. Photo by Janice Glime.

Habitat

One might expect that small fish like **minnows** would seek refuge or cover among large mosses like ***Fontinalis*** spp. But finding documentation about it is a challenge. Jones (1951) listed three small fish that used ***Fontinalis antipyretica*** (Figure 3) on bedrock as their habitat in a Welsh river: ***Phoxinus phoxinus*** (minnow; Figure 4), ***Gasterosteus aculeatus*** (three-spined stickleback, Figure 5), ***Barbatula barbatula*** (=***Nemacheilus barbatula***) (loach; Figure 6). He determined that fish mostly under 20 mm length preferred beds of moss and waterweed. Nevertheless, there was no evidence they ever ate the moss. Since fish like ***Phoxinus phoxinus*** may grow to 8-10 cm (Wikipedia 2012), it means that the mosses serve as a nursery – a place for the young fingerlings to hide from hungry predators.

Figure 3. ***Fontinalis antipyretica*** at the edge of a stream where it can provide cover for small fish. Photo by Andrew Spink at <http://www.andrewspink.nl/mosses/>, with permission.

Figure 4. ***Phoxinus phoxinus*** (minnows), fish small enough to hide among large mosses. Photo by Carlo Morelli, through Wikimedia Commons.

Figure 5. ***Gasterosteus aculeatus*** (three-spined stickleback). Photo by D. Ross Robinson, through EOL.com.

Figure 6. ***Barbatula barbatula***. Photo by Michal Maňas, through Wikimedia Commons.

In his study of mayfly life histories, Macan (1978) noted that ***Cottus gobio*** (bullhead) and ***Barbatula barbatula*** (stone loach) were taken in the moss samples. These mosses were colonies of ***Cinclidotus fontinaloides*** on permanently submerged rocks.

Spawning

Mills (1981) found that the roach (***Rutilus rutilus***; Figure 7) spawned in thick beds of ***Fontinalis antipyretica*** (Figure 3), placing their eggs throughout the fronds, but concentrating them away from the base of the moss and near the water surface, especially on those parts of the site that had relatively fast currents adjacent to the moss. This positioning afforded the eggs greater security against desiccation because the ends of the moss fronds could move up and down as the water level rose and fell.

Figure 7. **Roach** (***Rutilus rutilus***), a fish that is known to use the brook moss (***Fontinalis***) for spawning. Photo by T. Voekler, through Wikimedia Commons.

The roach spends larval steps 3-5 in water with macrophytes or woody debris, then moves out of the plant areas when it becomes older and larger (Copp 1990). Copp suggested that the young fish could perceive environmental change, as evidenced by their shift in habitat.

The pike-perch, ***Sander lucioperca*** (=*Stizostedion lucioperca*; Figure 8), so-named for its pointed nose, also will select mosses for nesting and spawning, in one case selecting the green parts of moss overgrown by bilberry, or moss and roots (Bastl 1969). Bastl recommended that such substrata can be used to improve spawning possibilities for this fish. These fish did not use the plastic strips provided as a substitute, so the moss must embody some beneficial property.

Figure 8. Pike-perch (***Sander lucioperca***). Photo by Piet Spaans, through Wikimedia Commons.

The spawning behavior of the pike-perch in natural habitats is poorly known (Lappalainen *et al*. 2003). One reason for this is the selection by the fish of murky habitats with 1-3 m depth, making them difficult to observe (Lappalainen *et al*. 2003; Zander 2010). Pike-perch typically inhabit deep, calm water of canals, lakes, reservoirs, and rivers (Luna & Bailly 2010). Their habit of feeding on other fish makes them a predator to hide from. The temperature of their habitat changes seasonally, forcing them to move to a different habitat. In autumn they prefer large pebbles in 1.2-1.8 m water, but as the temperature drops to 5ºC, they move to pits and trenches to spend the winter. In spring, a temperature of 2.8ºC signals the time to move upstream, where they spawn over large pebbles at 11ºC. Their pale yellow eggs attach to emergent vegetation or stones or gravel. The parents then drift downstream to pools, with many of the females dying after spawning.

The pike-perch can be a competitor of the roach, at least in lake habitats (Brabrand & Gaafeng 1993). Its presence can cause the roach to move from the open water to the littoral zone where vegetation is present. In this case, mosses such as ***Fontinalis*** could provide cover to protect the juveniles from predation by larger fish. But the littoral zone is not without its dangers. Perch (***Perca fluviatilis***; Figure 9) can eat the young fish and compete with them. However, in some situations there are sufficient Chironomidae (midge; Figure 10) larvae to feed the perch, and the perch don't bother the roaches (Persson 1987). One could suppose that if mosses are present, then Chironomidae are present (Glime 1994), and the mosses would provide a food source as well as protection. In this case, providing food for the predator of the roach is a bonus.

Figure 9. ***Perca fluviatilis***, a predator that drives fish to hide among dangling vegetation. Photo from Wikimedia Commons.

Figure 10. **Chironomidae**, illustrating their potential abundance. Photo by Simon Carmichael, through Creative Commons.

The things that show up when one does a Google search can be rather amusing, but sometimes one gets some real gems. More often, one must make some educated guesses and dig deeper. Such was the case in trying to find fish that use bryophytes for spawning. It seems logical that fish that use "vegetation" for spawning in mountain or rapid streams are likely to use mosses like ***Fontinalis*** species as an egg repository. But rarely is the "vegetation" identified further.

Wright, as early as 1901, recognized at least minimal vegetation differences when describing the spawning behavior of the "**stickleback**" (**Gasterosteidae**) in some detail. He noted that not all sticklebacks were the same and that their nest construction behavior differed. One variety (species?) makes a nest "like a muff among waterweeds." Another little fish collects straw, bits of grass, and moss with his mouth. He tucks these into the gravel and sand and presses them into place with his body. He then glues these with glue exuded from his own skin. This forms a floor, and he builds a small hut of woven fibers and moss. There is a small door at the top of the hut. The fish ultimately tests the strength of this hut by stirring up the nearby water with its tail.

The only other information I have found on nests of sticklebacks is 110 years later on a website (Coarse Fish 2011). In this case, the **nine-spined stickleback** (***Pungitius pungitius***; Figure 11), a circum-Arctic and widespread northern hemisphere fish of quiet water in streams, ponds, and lakes, uses "**willow moss**," a common name sometimes used for ***Fontinalis antipyretica***. The male ***P. pungitius*** builds the nest and cares for the young. The nest is near the bottom, typically built into the "vegetation." This is a tubular nest about 4 cm long and is made from threadlike algae and **willow moss**.

Figure 11. **Nine-spined stickleback** (***Pungitius pungitius***), a fish that occasionally builds its nest among ***Fontinalis antipyretica***. Photo through Creative Commons.

Nancy Auer (pers. comm. 20 Nov 2011), a larval fish expert, explains the scarcity of fish eggs among mosses. "Most moss is not that 'open' so adult fish may not use it and even larvae since most are in the water column."

Aquarium Fish

Aquarium fish keepers have discovered the advantages of adding aquatic mosses such as Java moss (which includes a variety of species, but is mostly ***Taxiphyllum barbieri***; Figure 12) for both decoration and spawning media (Benl 1958; Takaki *et al*. 1982). Axelrod and Vorderwinkler (1983) found that ***Fontinalis antipyretica*** var. ***gracilis*** (Figure 13) provided the best spawning grounds for certain tropical fish. The mosses also serve to provide hiding places for smaller fish being chased by larger ones or those fish that just prefer to hide during daylight hours.

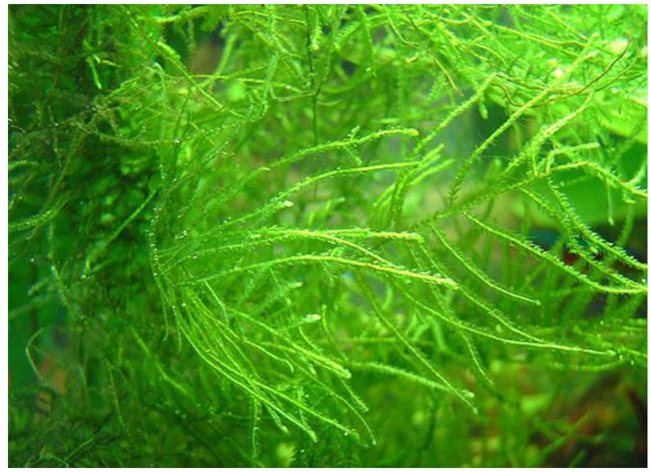

Figure 12. Java moss (***Taxiphyllum barbieri***). Photo by Buchling, through Creative Commons.

Figure 13. ***Fontinalis antipyretica*** var. ***gracilis***. Photo by Des Callaghan, with permission.

Bohlen (1999) used mosses in 40-liter aquaria to rear the spined loach (***Cobitis taenia***; Figure 14), a common freshwater fish of oxygen-rich water from Europe and Asia (Robotmam 1977). The fish laid their eggs in the most dense moss vegetation available (Bohlen 1999). The eggs lacked adhesion and easily fell through the gauze beneath the moss. Eggs numbering 2905-4282 were laid over a period of 101-120 days and were successfully reared using this method.

One website [Breeding my pencil fish (***Nannostomus beckfordi***; see Figure 15) 2007] provides a video of the golden pencil fish (***Nannostomus beckfordi***) breeding among the Java moss fronds in an aquarium. The pencil fish, widespread in its native South America (Wikipedia: Pencil fish), with a wide distribution in the lower Rio Negro and middle Amazonas river (AquaWorld: *Nannostomus beckfordi* 2011). It prefers slightly acidic water (pH 6.0-7.5), which is likewise suitable for many aquatic bryophytes. Java moss is especially good for scatter breeders, serving like a safety net to catch the eggs. The moss needs to be kept clean to remain healthy, but this cleaning may be detrimental to the eggs that are housed there, as they, too, may be removed.

Figure 14. Spined loach (***Cobitis taenia***). Photo by J. C. Harf, through Wikimedia Commons.

Figure 15. ***Nannostomus beckfordi***, a genus in which some members deposit eggs among mosses. Photo by Jan Ševčík, through EOL Commons.

The website Aquamoss extols the benefits of **Java moss** for rearing **killifish** (Figure 16-Figure 17), **barbs** (Figure 18), and **characins** (Figure 19). Not only does the moss provide cover, but it helps to keep the aquarium clean by absorbing the nitrogen waste. Eggs among the mosses are protected from predation, and the moss provides a substrate for bacteria, detritus, and other food sources. The author of the site also claims that the young fry grow better when Java moss is in the tank.

Figure 16. One of many kinds of killifish, ***Nothobranchius rachovii*** (**bluefin notho**). Photo by Andreas Wretström, through Wikimedia Commons.

Figure 17. ***Heterandria formosa***, the **least killifish**. Photo by Brian Gratwicke, through Creative Commons.

Figure 18. Tinfoil barbs (**Cyprinidae**). Photo from Wikimedia Commons.

Figure 19. Red phantom tetra, ***Megalamphodus sweglesi*** (Characidae). Photo from Wikimedia Commons.

A native southeastern USA fish, ***Elassoma evergladei*** (Figure 20), the **pygmy sunfish**, is a very skittish fish when it has no cover. In an aquarium, **Java moss** serves well to provide cover for this small fish. In the wild, it seeks shelter among the vegetation and prefers to lay its eggs on *Ceratophyllum demersum*. The cover helps to protect the males against the aggressive behavior of othe territorial (especially larger) males.

Java moss (***Taxiphyllum barbieri***; Figure 12) may be the best of the mosses for removing nitrogen in multiple forms (Alghamdi 2003), withstanding the wide chemical range of aquarium water, and doing well at warm temperatures, but other mosses have also been used successfully. Takaki *et al*. (1982) report the use of the mosses ***Amblystegium*** (***Leptodictyum riparium***; Figure 21), ***Fontinalis*** spp. (Figure 13), ***Platyhypnidium riparioides*** (Figure 22), ***Rhacopilum***, ***Taxiphyllum*** spp.

(Figure 12), ***Vesicularia*** (Figure 23), and the liverworts ***Riccia fluitans*** (Figure 24), ***Ricciocarpos natans*** (Figure 25), and ***Chiloscyphus*** (Figure 26). I have been successful in using ***Bryum pseudotriquetrum*** (Figure 27) in an aquarium with alkaline water. Beware of dealers selling a club moss as an aquarium plant. It is neither a moss nor an aquatic species. It is a tracheophyte (*Lycopodium obscurum*) that will retain its green color for several months under water. For more information on use of mosses for aquaria, see Chapter 4 (Aquaria) of Volume 5, Uses.

Figure 20. ***Elassoma evergladei*** (**pygmy sunfish**) with a species of "**Java**" **moss**. Photo by Brian Gratwicke, through Creative Commons.

Figure 21. ***Leptodictyum riparium***, a suitable aquarium moss. Photo by Tan Sze Wei, Aquamoss website <www.aquamoss.net>, with permission.

Figure 22. ***Platyhypnidium riparioides***, a suitable moss for an aquarium. Photo by Des Callaghan, with permission.

Figure 23. ***Vesicularia montagnei***, Christmas Moss, in an aquarium. Photo by Tan Sze Wei, Aquamoss website <www.aquamoss.net>, with permission.

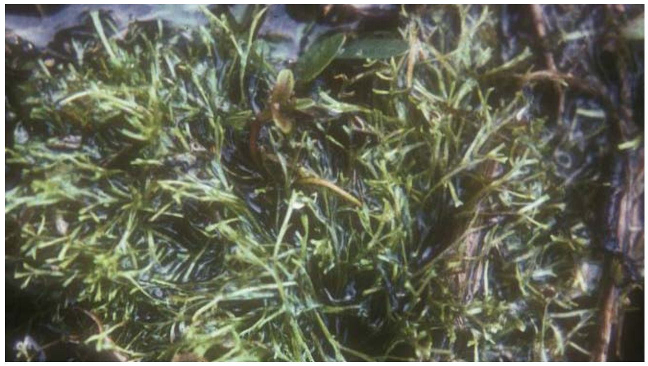

Figure 24. ***Riccia fluitans*** can be grown floating or in balls at the bottom of the aquarium in medium soft to hard water, *p*H 6-8, 15-30ºC (Aquatic Community). Photo by Janice Glime

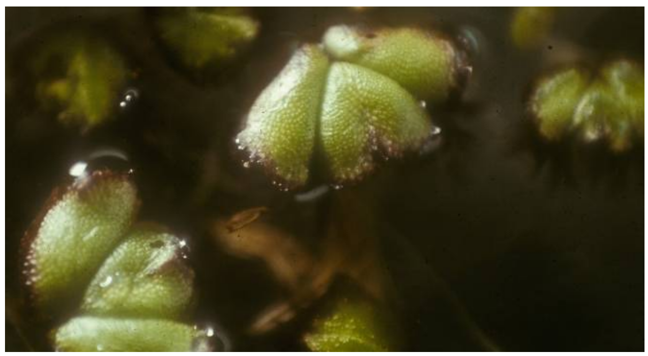

Figure 25. ***Ricciocarpos natans***, a floating thallose liverwort sometimes used in aquaria. Photo by Janice Glime.

Figure 26. ***Chiloscyphus polyanthos***, a leafy liverwort suitable for an aquarium. Photo by Jan-Peter Frahm, with permission.

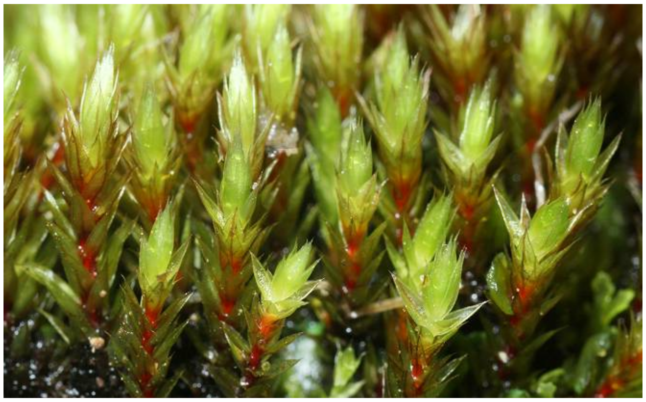

Figure 27. ***Bryum pseudotriquetrum*** (Marsh Bryum) grows in marshes and in shallow water at lake and stream edges. It can make an interesting small forest on the bottom of an aquarium. Photo by Barry Stewart, with permission.

Food

Bowden *et al*. (1999) pointed out that the roles of bryophytes in streams remain largely unexplored. Their role as a food source is one of these relatively unexplored areas. Specifically, they stated that it is "not clear whether fish benefit from an increase in abundance of insects often observed when bryophytes are present in a stream."

Cheney mentioned in 1895 that bryophytes serve as a food source for fish. Richards (1946) reported on the introduction of ***Fontinalis antipyretica*** into streams in South Africa in an effort to increase invertebrate populations that serve as fish food. Unfortunately, the insects in those streams were adapted to smooth rocks and bottom sediments and did not fare well on the rough structure of the mosses. Hence, their substrate was diminished and their numbers decreased. I know of no follow-up studies to see if this changed, with better adapted species arriving to fill the void.

Bryophytes can serve as a food source in two ways. The most obvious, but rarely used, is as a direct food source – eating the bryophyte. The other is that the bryophytes house numerous insects and other arthropods that serve as food. ***Fontinalis*** serves as a source of abundant food organisms, particularly chironomid larvae (Figure 10), for fish in the same stream (Mills 1981). Macan and Worthington (1974), in their book "Life in Lakes and Rivers," consider the mosses and liverworts that occur in thick mats to "profoundly influence fauna by providing a foothold for animals which otherwise could be swept away by curent."

Brusven *et al*. (1990) examined the importance of stream bryophytes as providers of drifting stream invertebrates that serve as potential fish food. They compared the density, biomass, and drift in various areas of the South Fork Salmon River, Idaho, USA, including areas with and without moss cover of ***Fontinalis neomexicana***. Insect densities were 4-18 times as great in moss clumps compared to moss-free areas. Simply being near the moss in mossy areas did not significantly increase invertebrate density compared to areas with no moss. And Brusven *et al*. were unable to determine any advantage to fish feeding in the daytime. It seems that despite the greater number of invertebrates living among the mosses, the daytime drift in that area was no greater than in the moss-free areas. That does not mean that there would be no differences at night when the greatest drifting occurs. If one assumes that daytime feeders only strike at drifting invertebrates, the mosses may not provide them with a feeding advantage until these invertebrates emerge as adults that fly above the stream within striking distance.

Muotka and Laasonen (2002) made it clear that retention of mosses was an important part of stream restoration in the channellized streams used for hauling out forest harvest, citing that when the mosses were dislodged they were replaced by periphytic algae and that only periphyton feeders increased when streams were restored by the addition of leaf litter that caused further loss of bryophytes.

Nurminen *et al*. (2003) explored the relationships of the rudd (***Scardinius erythrophthalmus***; Figure 28-Figure 29) and found that bryophytes were included among other aquatic macrophytes in their diet. In the period of 15 May to 15 June, bryophytes were more than half the diet by weight (26.2 g per g ww fish) for 6-year-old fish, but less for other ages and time periods. The **omnivorous** (eats everything) common rudd is widely distributed in South America, Europe, and middle Asia (Common Rudd 2010). It prefers clean water of lakes, ponds, large rivers, small streams, and even thermal springs, with lots of plant cover, where they can feed on the plants at warmer temperatures (above 18ºC). Early stage larvae start their diet on small algae, then shift to cladocerans and copepods, before including the broad range of immature insects and vegetation that characterize the adult diet.

Figure 28. The rudd (***Scardinius erythrophthalmus***), a fish that actually eats bryophytes. Photo from Wikimedia Commons.

Figure 29. Juveniles of the rudd (***Scardinius erythrophthalmus***). Photo by Piet Spaans, through Wikimedia Commons.

Hypostomus margaritifer (Loricariidae), a relative of the common aquarium plecostomus (Figure 30), in the Upper Paraná River, Brazil, uses bryophytes and red algae as its primary food (Delariva & Agostinho 2001).

Figure 30. ***Hypostomus plecostomus***, a common aquarium fish that feeds on attached algae. Photo from Wikimedia Commons.

At least one observation provides definite proof that some fish eat bryophytes. On the Aquamoss website, we are warned not to put the Siamese algae eater, ***Crossocheilus siamensis*** (Figure 31), in a tank with Taiwan moss (***Taxiphyllum alternans***; Figure 32) because the fish will devour it – quickly! (Figure 32) .

Figure 31. Siamese algae eaters (***Crossocheilus siamensis***) nibbling on Taiwan moss (***Taxiphyllum alternans***). Photo from Tan Sze Wei, Aquamoss website <http://www.aquamoss.net/Articles/Siamese-Algae-Eater-And-Aquatic-Moss.htm>, with permission.

Jones (1951) discovered that plant material (including algae) was only discernible in the first part of the gut, being digested and amorphous by the more distal portions. In that portion, only impervious parts like chitinous arthropod exoskeletons could be identified. He expressed concern that studies that did not recognize this would give misleading proportions of the food choices.

Frost (1942) recognized the importance of bryophytes in providing a habitat for food organisms of fish. She had already demonstrated that these organisms were important in the diet of **brown trout** (***Salmo trutta***; Figure 33) at both Ballysmuttan and Straffan in Ireland (Frost 1939). Young salmon have feeding habits similar to those of trout and similarly consumed a large portion of their food from moss dwellers (Frost & Went 1940). And many of the smaller minnows "cropped" the moss fauna (Frost 1942). Not only do the mosses provide shelter for the immature stages of these food organisms, thus providing food at that stage, but it is likely that some of the consumed aerial adult forms spent their younger aquatic days among the mosses.

Figure 32. Taiwan moss (***Taxiphyllum alternans***). **Upper:** Before the introduction of the Siamese algae eater (***Crossocheilus siamensis***) into the tank. **Lower:** One day after the introduction of the Siamese algae eater. Photos from Tan Sze Wei, Aquamoss website <http://www.aquamoss.net/Articles/Siamese-Algae-Eater-And-Aquatic-Moss.htm>, with permission.

Figure 33. **Brown trout** (***Salmo trutta***) on a stream bed. Photo through Wikimedia Commons.

We know that the roach (***Rutilus rutilus***; Figure 34), a common fish in lakes and lowland rivers, spawns in mosses (Mills 1981). From that we can easily deduce that at least some individuals live in places where mosses occur. Roaches consume aquatic insect larvae and molluscs as they grow (Mann 1973), but switch to mostly plant material and algae as they get larger (Hellawell 1972; Mann 1973). It is a natural extension in logic then, to infer that organisms that live among the mosses are potential food organisms, whether it is while they are in the mosses, or only when they venture forth into the open water. So far there seems to be no documentation that the plant material includes mosses, but certainly some of the moss inhabitants must be eaten.

Figure 34. Roach, ***Rutilus rutilus***. Photo by Andreas Hartl, through Creative Commons.

Sayre (1936) reports a case in which rainbow trout (***Onchorhynchos mykiss***, formerly *Salmo gairdneri*; Figure 1) actually eats mosses (not ***Fontinalis***, apparently). When insects become scarce in streams in autumn, mosses can become part of the diet. A few strands of ***Scleropodium obtusifolium*** were found in the gut of one of these normally carnivorous individuals in a stream on the western slope of Colorado, USA. Sayre considered that they switched to algae and mosses because other food sources were scarce. It is possible, however, that such invertebrates as Chironomidae were still abundant among the moss leaves. She reported that the moss had lost some color but had not been digested, adding further support to the suggestion that it was only housing the real food.

As one might expect, mosses provide camouflage and cover for potential fish-food organisms. A particularly interesting case is that of the dragonfly ***Leucorrhinia dubia*** (Odonata) (Henrikson 1993). The naiads of this insect are able to change color to match the brown and green of local ***Sphagnum*** (Figure 35). They are significantly more abundant among ***Sphagnum*** and show a preference for this substrate in lab tests. Where lakes have large ***Sphagnum*** mats, this dragonfly is able to co-exist with fish.

Fish serve as human food, and in Alaska the mosses played an important but misunderstood role in their preservation. The Alaskan natives stored their fish and whale blubber in holes and packed them into holes lined with wood, skins, or leaves and covered them with mosses or leaves (Segal 1992). These were left to ferment for 1-2 months. With the introduction of modern technology, many switched to using plastic bags instead of the natural products. The result was that often the anaerobic conditions of the bags fostered the growth of ***Clostridium botulinum***, resulting in an increase of botulism from 1.2 cases per 100,000 population before 1966 to 15.2 cases per 100,000 by 1992.

Figure 35. ***Sphagnum cuspidatum***, showing brown and green colors that are matched by the naiad of the dragonfly ***Leucorrhinia dubia***. Photo by Michael Lüth, with permission.

Piscicidal Properties

One reason for the refusal of fish to eat bryophytes may be the chemical properties of the mosses. Asakawa *et al.* (1985) found a diterpenedial in the liverwort ***Lobatoriccardia yakishimensis*** that is potent in killing fish! We know that many bryophytes have secondary compounds that discourage herbivory and it is likely that there are many more than this one that discourage fish from eating the bryophytes. The strongest of these **piscicides** seem to be the (-)-polygodial from the ***Porella vernicosa*** complex (Figure 36) and sacculatal from ***Trichocoleopsis sacculata*** (Figure 37) and ***Pellia endiviifolia*** (Figure 38), ***Pallavicinia levieri*** (Figure 39), and ***Lobatoriccardia yakushimensis***, all liverworts (Asakawa 2007). These two compounds have a hot taste and can kill **killifish** (***Oryzia latipes***; Figure 40) within 2 hours at a concentration of only 0.4 ppm. Sacculatal and 1β-hydroxysacculatal are lethal to the **killifish** within only 20 minutes at 1 ppm. On the other hand, isopolygodial and isosacculatal from the same liverworts seem to be harmless at concentrations of 10,000 ppm.

Figure 36. ***Porella vernicosa***, member of a liverwort complex that produces the piscicide polygodial. Photo by Masanobu Higuchi, with permission.

Figure 37. ***Trichocoleopsis sacculata***, a leafy liverwort that produces the piscicide sacculatal. Photo by Rui-Liang Zhu, with permission.

Figure 38. ***Pellia endiviifolia*** with young capsules. Photo by Michael Lüth, with permission.

Figure 39. ***Pallavicinia levieri***, a thallose liverwort that produces sacculatal, a piscicide. Photo by Rui-Liang Zhu, with permission.

Figure 40. ***Oryzia latipes***. Photo through Wikimedia Commons.

Among the bryophytes, liverworts have received the most attention regarding piscicidal and other antibiotic activities. This is because liverwort cells have oil bodies that store lipophilic terpenoids and aromatic compounds that serve these purposes (Asakawa 2001).

Cover

The most important role of bryophytes, from a fish perspective, may be that of cover. ***Fontinalis*** (Figure 41) species, with their long, dangling branches, is especially good at providing cover and rarely is out of water during breeding season.

Figure 41. ***Fontinalis antipyretica*** forming a dense mat of streamers that can provide cover for eggs and young fish. Photo by Michael Lüth, with permission.

But not all bryophytes are advantageous as cover. In Norway, Heggenes and Salteit (2002) found that juveniles and adults of Atlantic salmon (***Salmo salar***; Figure 42) were less dense in areas where liverworts grew than where that bryophyte had been removed. They suggested that increases in liverwort density actually had a negative effect on the Atlantic salmon. Removal of the brook moss ***Fontinalis*** (Figure 41) had no significant effect on density of salmon. Brown trout (***Salmo trutta***; Figure 43-Figure 44), on the other hand, had higher densities in association with the ***Fontinalis***.

Figure 42. Atlantic salmon (***Salmo salar***). Photo by William Hartley, USFWS, through public domain.

The Atlantic salmon (***Salmo salar***) is one of those anadromous fish that migrate upstream to spawn, then the young fish return to salt water until breeding time (Atlantic Salmon 2010). Once independent of the yolk sack, the juveniles begin eating tiny invertebrates, but as they become larger they eat small fish. Aquatic insects are a common food, and bryophytes can serve as either direct sources of the insects, or cover for these insects when they are not in open water. In any case, bryophytes generally increase numbers of insects in streams (see later chapter on aquatic insects).

The brown trout (***Salmo trutta***; Figure 43-Figure 44) likewise migrate upstream to spawn, but in this case they are migrating from lakes (Brown trout 2010). While in the streams or rivers, they are major predators on macroinvertebrates – shrimp, corixids, caddisflies, stoneflies, and mayflies. Cover is important protection from predators for them and they seek out submerged rocks, undercut banks, and overhanging vegetation, which could include mosses.

Figure 43. Brown trout (***Salmo trutta***), a fish that benefits in density from the presence of ***Fontinalis***. Photo by Jason Neuswanger at Troutnut.com, with permission.

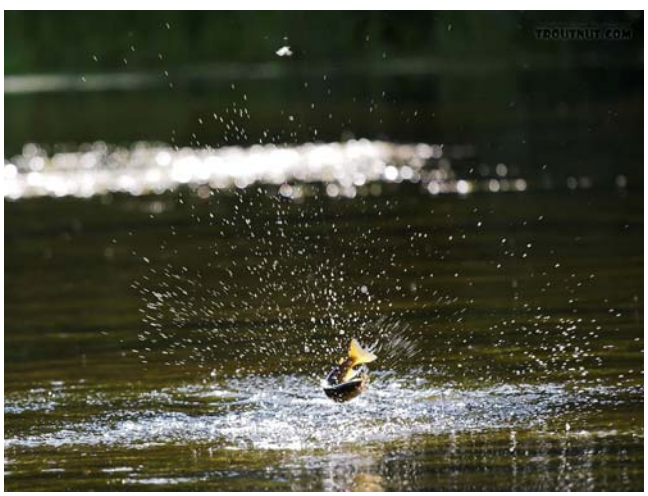

Figure 44. Brown trout (***Salmo trutta***) jumping. Photos by Jason Neuswanger at Troutnut.com, with permission.

Douglas Burns (2008) tells about his friend who finds successful fishing for bass at strip mine ponds covered with moss. The only problem seems to be finding open water in which to work the lure. The advantage to those fishing is that these ponds are very productive and rarely have other persons fishing.

In Volume 5 on Uses, Chapter 4 (Aquaria), I have discussed the use of bryophytes in aquaria. For example, Tan (2003) reported that the Java moss (mostly ***Taxiphyllum barbieri***; Figure 12, Figure 31, Figure 32) is used by fish hobbyists around the world to decorate aquaria and provide cover.

Diversity

With the cover provided by bryophytes, one would assume there would be some correlation between fish communities and bryophyte cover. However, when Paavola (2003) tested this in an Arctic stream, there seemed to be little protective relationship. Rather, fish communities seemed to relate to oxygen levels, depth, and stream size, whereas bryophytes were more related to nutrient levels and in-stream complexity. Species richness did seem to correlate somewhat.

It appears that mosses might be able to help some fish survive drought conditions. McPhail (1999) experimented with the black mudfish (***Neochanna diversus***; Figure 45 - Figure 46) from New Zealand to determine how it might survive both hypoxia and drought. This fish is able to breathe air by rising to the surface and gulping an air bubble that it holds in the buccal cavity while still using its gills to get oxygen to its blood. In McPhail's study, when the water around it dropped to less than 2.5 mg L^{-1}, the fish all gulped air from the surface. At temperatures around 20-22ºC, the animals stayed alive on damp mosses for 10 weeks. They lost weight steadily, but all adults recovered upon re-immersion. Two young-of-the-year fish died. The black mudfish is on the IUCN Red List of Threatened Species and was thought to be extinct, but in a 2004 survey in New Zealand, a healthy population was found (World Conservation Monitoring Centre 1996). McPhail (1999) suggested that as a management strategy, mosses could be provided in restoration to help fish survive periods of drought.

Figure 45. Brown mudfish, ***Neochanna diversus***. Photo by R. M. McDowell (NIWA), with permission.

Figure 46. Brown mudfish, ***Neochanna diversus***, showing its small size. Photo by Vince Kerr, permission pending.

Heino *et al.* (2005) and Paavola *et al.* (2003) found that bryophytes were not a good surrogate for fish diversity. Rather, species richness of this group seems to more related to geographic location, stream size, water color, and acidity. Hence, bryophytes are apparently not useful in predicting fish diversity. Paavola *et al.* (2006) further clarified this poor relationship by examining 101 boreal streams for concordance among fish, macroinvertebrates, and bryophytes. They found that spatial extent of the study was a critical factor in predictability (*i.e.* concordance) and that single river systems provided poor concordance.

Biodiversity of bryophytes can be threatened by fish-harvesting activities (Russell 2006). In the southernmost province of Chile, bryophytes are threatened by fish farming, among other things human activities.

Nutrient Relations

But are the bryophytes really a source of nutrition for the fish?

Sayre (1936) and Bland (1971) state that in Colorado streams rainbow trout will eat mosses when insects become scarce, but when we tried to feed ***Fontinalis*** to starved laboratory-reared rainbow trout (***Onchorhynchos mykiss***, formerly *Salmo gairdneri*), we were successful only occasionally when our graduate student forced the moss into their mouths (Paulson 1980). In the few cases where he was successful in force-feeding them, they later passed a small, cylindrical package of ***Fontinalis*** (Figure 47), essentially in tact, at the other end of the digestive tract! If they eat it in nature, it may be to get the insects that invariably live among the leaves.

Figure 47. Package of feces from rainbow trout (***Oncorhynchus mykiss***) containing undigested ***Fontinalis*** that had been force-fed. Photo by Janice Glime.

There does not seem to be any evidence that fish get nutrients from the bryophytes themselves. On the other hand, bryophytes may get nutrients from the fish! Peterson and Matthews (2009) found that the annual migration of salmon back to their streams can carry nutrients from the ocean to the streams. Using changes in ^{15}N, they measured C:N and C:P ratios in the bryophytes, among other things. When they compared channels with and without decomposing salmon, the bryophytes had lower C:N and C:P ratios in channels with salmon decomposing than in those without. This ratio is the result of higher N and P content, *i.e.*, more nutrients were stored in bryophytes of streams where the salmon returned during migration. Thus, bryophytes contribute to the capture of salmon-derived nutrients in the streams.

Movement of nutrients upstream in fish and ultimate arrival in bryophytes might be predictable, but finding ocean nutrients in **riparian** (banks of a natural water course) bryophytes is a bit of a surprise. Ben-David *et al.* (1998) found salmon-derived nutrients along forest trails near streams. Wilkinson *et al.* (2005) suggested that these nutrients are important contributions to the nutrient input of non-vascular plants. Bryophytes such as ***Hylocomium splendens*** absorb up to 90% of the dissolved nutrients. Through this pathway, the bryophytes retain nutrients that may later be released to the tracheophytes.

*p*H and *Sphagnum*

All is not well in ***Sphagnum*** land as far as fish are concerned. Dunson and Martin (1973) looked at the effects of this moss on downstream communities of fish. They examined the effects of *p*H on the fish through transplant experiments and distribution data. Brook trout (***Salvelinus fontinalis***; Figure 48 - Figure 49) of various ages were transplanted upstream, near the bog, where the *p*H was lower. The two adult trout both died within seven days in the zone closest to the bog (*p*H down to 3.7). For smaller fish (5 cm), half were dead in 4.5 days and all of them after 10 days, while the *p*H generally remained above 4.4. In a second experiment, the *p*H generally remained below 4.4 and all 50 fish (5 cm) died within 6.3 days. Although other factors could account for the deaths (differences in flow rate, stress from transplantation, confinement), these data suggest that low *p*H resulting from ***Sphagnum*** could be detrimental to some fish populations.

Figure 48. Brook trout, ***Salvelinus fontinalis***, a fish sensitive to low *p*H. Photo by Derek Ramsey, through Wikimedia Commons.

Figure 49. Brook trout (***Salvelinus fontinalis***). Photo through public domain at EPA website.

Hinder *et al.* (1996) found that liming improved the quality of water downstream from peatlands by raising the *p*H. Brown trout (***Salmo trutta***; Figure 43-Figure 44) survived even after the *p*H dropped back down to 5.2-5.3.

Table 1. Presence (+) of four fish species at increasing distances and *p*H downstream from Bear Meadows Bog in Pennsylvania, USA. Data from Dunson & Martin 1973.

	1	2	3	4	5	6	7	tributary
Brook trout (*Salvelinus fontinalis*)				+	+	+	+	+
White sucker (*Catostomus commersoni*)					+	+	+	+
Creek chub (*Semotilus atromaculatus*)						+	+	+
Blacknose dace (*Rhinichthys atratulus*)						+	+	+
Lowest *p*H	3.7	3.7	-	4.0	4.2	4.2	5.1	5.3

Pollution

Mosses are known for their ability to absorb and concentrate heavy metals. Huckabee and Blaylock (1972) demnstrated this mercury. Caines *et al*. (1985) demonstrated that both mosses and liverworts could decrease the metal concentrations in associated water, but that as the H^+ ion concentration increased in the water, the ability of mosses to bind the metal ions decreased. This is consistent with experiments done with ***Sphagnum***; flooding that moss with H^+ ions is one way to remove its attached cations. In the Scottish streams, Caines *et al*. found that the metal ions in the mosses remained there as long as the *p*H remained above 5.5. But if the stream *p*H drops below that level due to acid rain or drainage from peatlands, it can cause sufficient release of heavy metals to be lethal to fish.

Concentration of the heavy metals by macro-invertebrates can be even higher than that in bryophytes, depending on their position in the food web (Culioli *et al*. 2009). But fish, despite depending on smaller organisms for food, retained the smallest concentrations of arsenic, even lower than that in water. Mersch *et al*. (1993) likewise found that the aquatic moss ***Fontinalis antipyretica*** had much higher concentrations of heavy metals than did fish. In fact, for fish the concentration depended on the tissue, with copper accumulating in the liver and lead in the kidney. Mouvet *et al*. (1993) reported four different instances in which fish were killed but mosses survived, supporting the notion of using mosses as biomonitors of stream health.

If mosses live and fish die, the mosses need to give some sort of early warning. One such warning is loss of green color. Other symptoms include the discoloration of the terminal bud. And for those willing to do the testing, measuring accumulation of suspected toxins in the moss can indicate the degree of accumulated pollution.

Lithner *et al*. (1995) compared the ability of invertebrates, fish (***Perca fluviatilis***, ***Esox lucius***), and ***Fontinalis antipyretica*** at a location in Sweden to sequester and concentrate heavy metals as a function of *p*H. The found that when the *p*H decreased, so did the bioconcentration factor for Zn, Cd, Ni, Co in bryophytes, but the concentrations of Pb and Cu increased in fish with decreasing *p*H. This emphasizes the fact that bryophytes and other organisms may not be surrogate indicators for the suitability of heavy metal conditions for at least some fish.

A new twist on the use of **mosses** associated with **fish** is related to the administration of antibiotics to cattle and **fish** (Pouliquen *et al*. 2009). Oxolinic acid, florfenicol, flumequine, and oxytetracycline are all used in farming both fish and cattle. These ultimately end up in "freshwater." A study in France reveals the ensuing scenario. In this case, four fish farms and a sewage plant were located on the main course of the river. The famous mossbags were used, this time in the water. All four of these antibiotics could be measured in the bryophytes and sediments, but not in the water. Both Flumequine and oxytetracycline entered the water from fish farms, animal farms, and possibly human pharmaceutical sources. Accumulations of antibiotics could, through the course of time, alter the flora and fauna of the river. If carried into drinking water, antibiotics could affect the digestive bacteria needed by humans and other animals. And the impact on native mammals that drink from the river could be a concern. Therefore, bryophytes could serve as suitable organisms for testing to determine the levels of antibiotics in the water, particularly when the events of these entering the river are intermittent. The bryophytes, as accumulators, can permit assessment over a lengthy period of time.

Global Warming

The controversial global warming may have an indirect effect on fish that is mediated by changes from planktonic algae to deep-water bryophytes (Felley 2003). Loss of organic carbon in lakes of the southern boreal foerst of Ontario, Canada, previously depleted by acid rain damage, results in clearer water. Lake levels are falling due to declines in rainfall and increased evaporation due to increased temperatures. These factors, and the greater penetration of light, have depressed the planktonic algae in favor of the deep-water (down to 50 m) **bryophytes**. The lakes are now too warm for the cold-loving **trout** that previously lived there. This signals danger for the Arctic lakes that typically remain cold far into the summer. Warming there could seriously affect the fish populations adapted for cold water.

Surrogate Species

Surrogate species are those that can be used to assess the conditions of a habitat in lieu of another species or group. Virtanen *et al*. (2009) attempted to determine the usefulness of **bryophytes** in this role, compared to two groups of insects, the **Chironomidae** (midges) and four orders of insects, **Ephemeroptera**, **Plecoptera**, **Trichoptera** and **Coleoptera**. They found that the bryophytes were not good surrogates for spring insects. On the other hand, there seemed to be relatively good agreement among bryophytes, benthic insects, and fish in boreal headwater streams across a broad scale of water drainage systems, but not at the fine scale of streams in a single drainage system. Such research suggests that bryophytes could be used to assess the likely success rate of introducing fish into streams that have lost portions of their native fauna.

Summary

Bryophytes can provide cover, food, and spawning ground for fish. Although it seems that few fish eat bryophytes, many fish food organisms live there. In those cases where the fish eat the bryophytes, it is not clear whether they gain any nutrition from them. Little fish can take cover in bryophytes. And at least some fish use bryophytes for spawning sites. One variety of stickleback builds a hut in which mosses can be a major constituent. Others simply uses the mosses as they are growing. Some liverworts, including streambank species, are known to have **piscicidal** properties, but their ability to use these in habitats where the fish occur is not known.

A number of mosses, especially Java moss (***Taxiphyllum barbieri***), are used in aquaria for cover and spawning beds. Furthermore, Java moss is able to remove the fish nitrogen waste from the water.

Some insects can only survive fish predation when they have cover among mosses, and the naiads of ***Leucorrhinia dubia*** are able to change color to blend in with the ***Sphagnum***.

Sphagnum can acidify lakes and streams, making them uninhabitable for at least some kinds of fish.

Bryophytes can benefit fish as biomonitors, providing early warning signs that the water is contaminated, including more recent contamination with antibiotics. But sometimes the ability of bryophytes to accumulate substances differs from that of the fish.

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